DTIC FILE COPY

DTIC
ELECTE
MAR 07 1990
S D
D

AD-A219 077

Limnol. Oceanogr., 33(3), 1988, 339–351
© 1988, by the American Society of Limnology and Oceanography, Inc.

In situ settling behavior of marine snow[1]

Alice L. Alldredge and Chris Gotschalk

Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara 93106

Abstract

The settling velocities of undisturbed macroscopic aggregates known as marine snow were measured with SCUBA in surface waters off southern California and analyzed as a function of aggregate size, mass, and density. The mean settling velocity was 74 ± 39 m d^{-1} for aggregates ranging from 2.4 to 75 mm in maximum length. Sinking rates in the field varied exponentially with aggregate size and dry weight and were consistently up to four times slower than rates measured in the laboratory.

The excess densities of the 80 aggregates examined were calculated from volume and dry weight and ranged over four orders of magnitude with a median of 1.4×10^{-4} g cm^{-3}. Aggregates of marine snow sank more slowly than predicted for either solid or porous spheres of equivalent volume and density, although their velocities were within the range expected for equivalent sinking prolate ellipsoids. No relationships between settling velocity and either excess density or particle shape were found. Drag coefficients of marine snow were also higher than predicted by theory for spheres of equivalent volume and density. These deviations from theoretical expectations may be partially explained by errors in the estimation of the excess densities of aggregates. Variability in the densities of the heterogeneous primary particles comprising marine snow (fecal pellets, clay-mineral particles, phytoplankton, molts, etc.) and the potential for buoyancy regulation by individual phytoplankton cells inhabiting aggregates make determination of excess density especially problematic.

Large, rapidly sinking particles are far less numerous than fine suspended particles in the pelagic zone of the sea. However, recent studies suggest that large particles are primarily responsible for the vertical transport of biogenic materials and elements through the water column (*see* Fowler and Knauer 1986). Although fecal pellets are a major source of large, rapidly sinking particles in some regions of the world's oceans (Angel 1984), in most other areas flocculent amorphous aggregates >0.5 mm in diameter, known as marine snow, appear to be the major source of particulate flux (Fowler and Knauer 1986).

Sinking aggregates transfer energy and nutrients from the surface mixed layer into the ocean interior and to the seafloor. The rate at which this transfer occurs depends primarily on the composition, size, abundance, and sinking rate of the particles. Although settling velocities of marine snow, ranging from 1 to 370 m d^{-1}, have been measured directly in both the laboratory (Silver and Alldredge 1981; Taguchi 1982; Gorsky et al. 1983) and the field (Shanks and Trent 1980) and estimated from in situ photographs (Billett et al. 1983; Lampitt 1985; Asper 1987), the relationships between settling velocity and aggregate properties such as size, mass, and density are not known. Accurate estimates of flux based on particle abundances in nature require information on size-specific sinking rates. Moreover, data on the settling behavior of aggregates are necessary in order to understand the quantitative impact of processes that alter aggregate size and density (consumption by grazers, dissolution, disaggregation, etc.) on the biogeochemical processes associated with particles in the water column. In this paper we present the first data on the settling behavior of undisturbed aggregates of marine snow in situ as a function of aggregate size, mass, and density. We discuss variations in this settling behavior from predicted theory and provide evidence that laboratory studies substantially overestimate sinking rates of marine snow in nature.

We thank V. Fabry, D. Campbell, S. Schoen, and C. Dolstra for diving assistance and M. Tulin for valuable discussion. We

[1] Supported by ONR contract N00014-85-k-0771. Contribution 114 to the Catalina Marine Science Center, University of Southern California.

90 03 05 030

especially thank S. MacIntyre, B. Logan, P. Komar, and three anonymous reviewers who made improvements to the manuscript.

Methods

Theoretical considerations—When a particle settles at a constant, or terminal, velocity through a fluid, the force of gravity pulling the particle downward is exactly balanced by the retarding drag force of the fluid flowing around the particle. The resulting force balance equation takes the form

$$V(\rho_a - \rho_f)g = \tfrac{1}{2}C_D A \rho_f U^2 \quad (1)$$

where V is the volume of the particle in cm^3, ρ_a the density of the particle in g cm^{-3}, ρ_f the density of the fluid in g cm^{-3}, g the acceleration due to gravity or 980 cm s^{-2}, A the maximum cross-sectional area of the particle perpendicular to the direction of sinking in cm^2, U the settling velocity of the particle in cm s^{-1}, and C_D (the drag coefficient) a dimensionless number. For spherical particles, C_D is a function of Reynolds number (Re $= dU/\nu$, where d is particle diameter in cm and ν is the kinematic viscosity of the fluid). At Reynolds numbers <0.5, Stokes' expression for a settling sphere is valid and $C_D \cong 24/\mathrm{Re}$ (White 1974). For nonspherical particles, such as marine snow, however, the drag coefficient becomes a complicated function of both shape and Reynolds number. This function must usually be determined empirically (*see* Tietjens 1957; Graf 1971; Komar and Reimers 1978). Rearranging Eq. 1 yields

$$U = (2g\Delta\rho V/\rho_f C_D A)^{1/2} \quad (2)$$

where $\Delta\rho = (\rho_a - \rho_f)$. From Eq. 2 we would expect the terminal settling velocity of an aggregate of marine snow to be a function of the excess density of the particle, the ratio of volume and projected area (in the direction of settling), and the drag coefficient. We measured the physical properties of marine snow appropriate for elucidating these relationships.

Since the drag coefficient and, thus, settling velocity are a function of shape, we also required a coefficient that adequately describes the shape of an aggregate and how it departs from spherical. Most previous studies of the effects of shape on the settling of natural particles, including sediment grains (Komar and Reimers 1978) and small animals such as foraminifera (Fok-Pun and Komar 1983), have used the Corey shape factor (CSF) (Albertson 1953; *see* McNown and Malaika 1950):

$$\mathrm{CSF} = \frac{D_s}{(D_i D_l)^{1/2}} \quad (3)$$

where D_s, D_l, and D_i are the smallest, largest, and intermediate axial diameters of the particle. For a spherical shape, CSF = 1. The further from spherical a particle becomes, the closer to 0 CSF becomes. McNown and Malaika (1950) found that the ratio of the principal-axis lengths was the best predictor for determining the effect of shape on the settling velocities of small ellipsoids, cones, cylinders, and prisms up to Re of ~ 10.

The simplest way to consider the effects of shape on settling velocity is to consider a sphere deformed to form a new shape of equivalent volume and density, encountering a different resistance from the fluid flow past it. This resistance differs from that of the original sphere by k, the coefficient of form resistance (also called the dynamic shape factor) where

$$k = \frac{U_s}{U} \quad (4)$$

with U_s the sinking velocity of a sphere of equivalent volume and density and U the settling velocity of the particle. Theoretical derivation of k and further discussion of the effects of particle shape on it can be found elsewhere (McNown and Malaika 1950; Davis 1979; Hutchinson 1967). For ellipsoids of regular shape, k varies as a direct function of CSF. Most prolate (largest axial diameter parallel to flow) ellipsoids and all oblate (largest axial diameters perpendicular to flow) ellipsoids have a $k > 1$ and sink more slowly than equivalent spheres. The further from spherical the particles become the larger k becomes (McNown and Malaika 1950).

Empirical measurements—Settling velocities of individual aggregates of marine snow were measured both in situ and in the laboratory. Field measurements were made at depths of 10–15 m during 25 SCUBA dives in the San Pedro Basin, California (4 km due east of Two Harbors, Catalina Island), in March and June 1986 and during two dives in the Santa Barbara Channel (6 km due south of the University of California, Santa Barbara) during July 1986. All dives were in late morning. We measured the settling velocities of 80 undisturbed aggregates of marine snow relative to a spot of dilute, neutrally buoyant fluorescein dye placed 3 cm below each particle. The powdered dye was mixed with seawater at depth so as to produce a solution of the same density as the seawater surrounding the aggregates. A SCUBA diver delivered the spot of dye (a few millimeters in diameter) from a dye ejector consisting of a hypodermic needle mounted on a 1-m-long, 2.4-cm-diameter plastic pipe (Fig. 1). The stock of this dye ejector rested against the diver's shoulder to stabilize the ejector and reduce vibration at its tip.

The 3-cm distance was determined by siting the bottom of the aggregate at the tip of a thin wire attached to the ejector exactly 3 cm above the release point of the dye (Fig. 1a). The dye spot congealed and stabilized in shape and size within 1–2 s after delivery. Several minutes were required for it to diffuse. With care, a diver could deliver a spot of dye, slowly pull the ejector back, and hang suspended 2–3 m from the aggregate without producing turbulence near the aggregate. Turbulence was easily detected by observing deformation of the dye spot. A second diver, located 7–8 m away, measured with a stopwatch the time required for the particle to sink to the dye spot, relying on visual cues from the first diver. This second diver then photographed the still undisturbed aggregate to provide a record of its size and shape using a Nikonos camera with a 1 : 1 or 3 : 1 close-up extension tube and framer. The aggregate was then collected in a 6-ml plastic cylinder for later determination of aggregate dry weight.

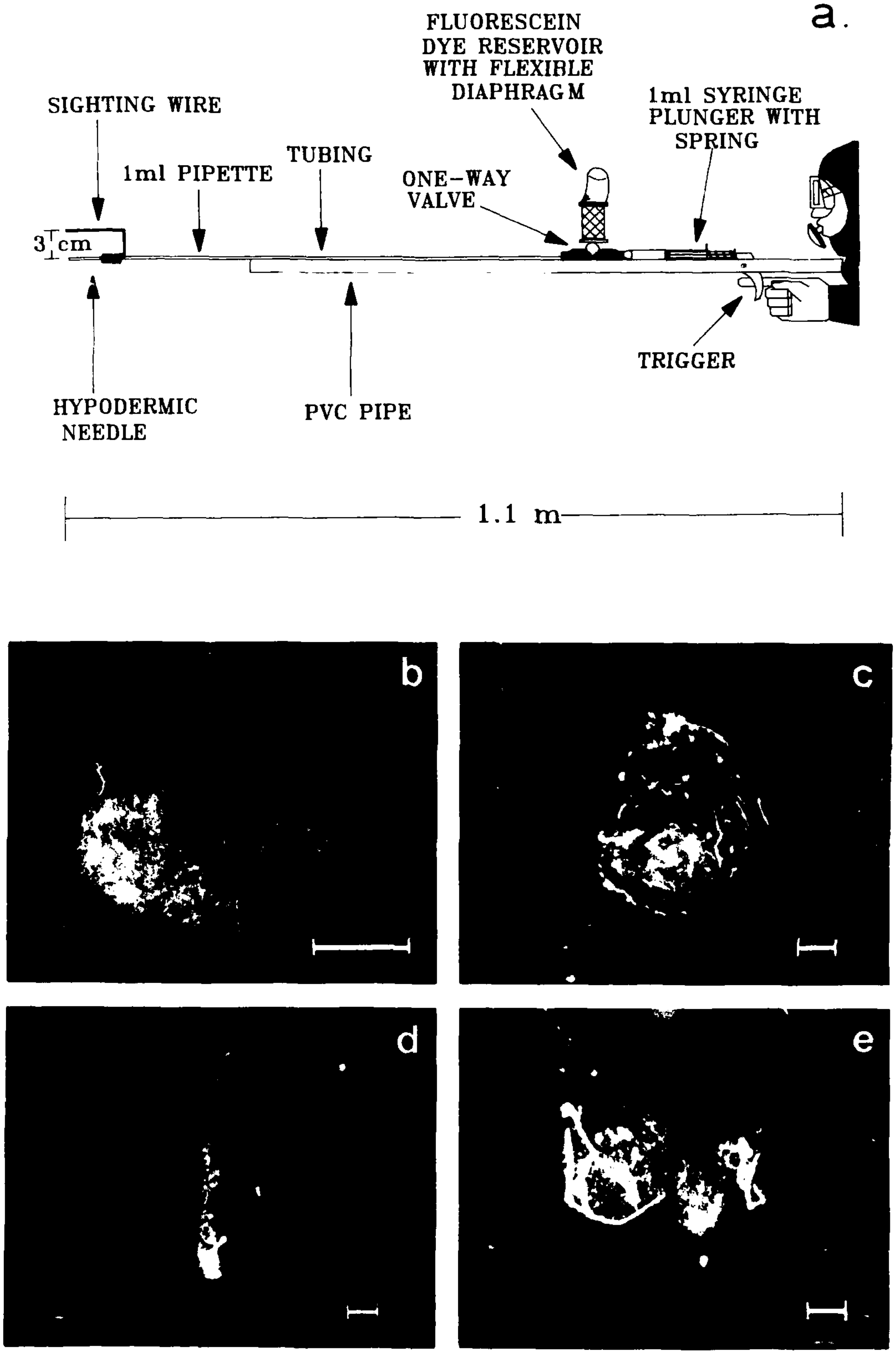
A single photograph was taken in a plane parallel to the direction of sinking (i.e. a side view) by orienting the particle at a predetermined focal distance from the camera lens demarcated by a thin wire frame. A transparent metric ruler photographed in the frame yielded scale. Turbulence produced by moving the camera after the first photograph altered the aggregate's shape and in some cases threatened to break the particle apart. These factors thwarted our attempts to obtain additional photographs in other planes. Direct observation of many aggregates in the field indicated, however, that most sinking aggregates are shaped like comets or prolate ellipsoids and are nearly symmetrical about their polar axes (parallel to the direction of sinking). Thus, a photograph oriented parallel to the plane of sinking allowed for the most accurate estimation of volume.

The settling velocities of 37 different aggregates were determined in the laboratory for comparison with field measurements. Aggregates of marine snow collected from 10-m depths in the Santa Barbara Channel were allowed to sink slowly out of the open bottom of their collecting cylinders into the top of an 8-cm-diameter, 2,000-ml graduated cylinder containing seawater from the depth of collection. Both the samples and the graduated cylinder were maintained in an environmental chamber at ambient seawater temperature (16°C), and settling rates were determined within 4 h of sample collection. Periodic injection of fluorescein dye into the settling chamber indicated that no convective currents were present. We timed the sinking of each aggregate past external markings on the graduated cylinder with a stopwatch. Each aggregate was then removed from the chamber with a pipette and placed on a filter for dry weight determination. Dry weight was used as the property of marine snow potentially least affected by collection and handling.

Physical characteristics of each sinking aggregate were determined as follows—

Dry weight: Each individual aggregate was filtered with 3 ml of surrounding seawater onto a preweighed Nuclepore filter (2.4-cm diameter, 0.40-μm pore size), rinsed quickly with distilled water and dried for a minimum of 24 h in a desiccator. Filters were reweighed to the nearest 0.1 μg on a Cahn electrobalance and the dry weights were corrected with 3-ml seawater blanks. Reweighing of some filters 10 d after placement in the desiccator indicated that all water was lost within the first 24 h.

A-1 21


a.
FLUORESCEIN DYE RESERVOIR WITH FLEXIBLE DIAPHRAGM
SIGHTING WIRE
1ml SYRINGE PLUNGER WITH SPRING
TUBING
1ml PIPETTE
ONE-WAY VALVE
3 cm
HYPODERMIC NEEDLE
PVC PIPE
TRIGGER
1.1 m
b
c
d
e

Diameter: The maximum diameter perpendicular to the direction of sinking was measured to the nearest 0.1 mm on the photographs.

Maximum length: The maximum length was measured to the nearest 0.1 mm on the photographs.

Projected area: Drag on a sinking particle may be correlated with the maximum cross-sectional area perpendicular to the direction of sinking. We calculated this projected area with the measured maximum cross-sectioned diameter assuming that this area was a circle. Photographs taken perpendicular to the direction of sinking would have yielded the projected area. Photographing small, fragile objects from directly above or below, however, is nearly impossible for a diver floating in open water. Moreover, such photographs would have yielded underestimates of volume since most aggregates were elongated along their polar axes.

We estimated the error involved in calculating the projected area from the maximum cross-sectional diameter using 30 three-dimensional clay models resembling the shapes of aggregates in our photographs. These models were 4–5 cm long, radially symmetrical, and molded to approximate the shape of the aggregates as seen from the side view in the photographs of the natural aggregates. The projected area of each model was determined from its maximal cross-sectional shadow perpendicular to the polar axis. That area was then compared with the calculated area of a circle having a diameter equal to the maximum cross-sectional diameter of the model. The 95% C.L. of the mean on our projected area measurements was ±19%.

Volume: Volume was calculated from the photograph of each aggregate, assuming that aggregates were symmetrical about their polar axis and that their volumes approximated ellipsoids or spheres. The few irregularly shaped aggregates, such as that shown in Fig. 1e, were divided into subunits resembling spheres, cylinders, or ellipsoids, and total volume was estimated by adding the volumes of these subunits. We also estimated the error of calculating volume from two-dimensional photographs using the clay models. We calculated the volume of these clay models from their two-dimensional shadows projected in the plane parallel to their polar axes and compared these calculated volumes with the actual displacement volumes of the models in water. These trials yielded a 95% C.L. on volumes of ±30%.

Porosity: Porosity is the fraction of an aggregate not occupied by solid matter and was needed to determine aggregate density. We calculated porosity, P, directly from the measurements of volume and dry weight with the equation:

$$P = 1 - \frac{W/\rho_s}{V} \tag{5}$$

where W is dry weight in g and ρ_s the density of the solid hydrated matter within the aggregate. We assumed $\rho_s = 1.23 \text{ g cm}^{-3}$ which is the wet density of euphausiid fecal pellets (Komar et al. 1981). Since zooplankton fecal pellets contain a representation of many of the types of particles found in marine snow including diatom frustules, clay-mineral particles, and intact cells, their wet density seemed a reasonable choice for the density of the solid matter within aggregates. By comparison, the density of dry cellulose is about 1.5 g cm^{-3} and that of living phytoplankton may be equal to seawater, about 1.025 g cm^{-3} (Smayda 1970). Since aggregates were generally >99% porous, our calculated porosities were not particularly sensitive to the value of ρ_s. Values of ρ_s 0.2 g cm^{-3} higher or lower than the value used altered porosity of our aggregates only negligibly.

←

Fig. 1. Measurement of sinking rates of marine snow in situ. a. Dye ejector used by SCUBA diver to deliver neutrally buoyant dye spot below aggregate. b. Aggregate formed from senescent diatoms and diatom frustules (scale = 1 cm). c. Spherical mucus aggregate formed from the decomposing house of an appendicularian. d. Comet-shaped aggregate of unknown origin. e. Irregularly shaped aggregate of unknown origin containing numerous macrocrustacean fecal pellets (scale of c–e = 1 mm).

Excess density ($\Delta\rho$): The difference between the density of the aggregate and that of the surrounding seawater was calculated from

$$\Delta\rho = \frac{W}{V}\left(1 - \frac{\rho_f}{\rho_s}\right). \quad (6)$$

Seawater density was determined from ambient temperature and salinity according to Mamayev (1975). Salinity was measured with a Plessey Environmental Systems laboratory salinometer (model 6230N).

Significant functional relationships between the above variables were determined with methods of standard linear regression (Sokal and Rohlf 1969).

Results

Characteristics of marine snow—Of the 80 aggregates of marine snow studied in the field, 68 were collected in the San Pedro Basin at a salinity of 33.570‰, a temperature of 15.0°C, and a seawater density of 1.02488 g cm^{-3}. The remaining 12 were from the Santa Barbara Basin at a salinity of 33.642‰, a temperature of 16.0°C, and a seawater density of 1.02466 g cm^{-3}. Data from the two study sites were pooled.

The 80 aggregates of marine snow were highly variable in size, shape, and general appearance. The 12 aggregates from the Santa Barbara Basin were all flocculent conglomerates of living senescent diatoms, particularly chain-forming species, and frustules (Fig. 1b) which formed following a diatom bloom (*see* Smetacek 1985). Aggregates from the San Pedro Basin were of diverse origins and appearance. Some were the remains of appendicularian houses containing considerable gelatinous mucus (Fig. 1c). Most were aggregates of smaller particles, detritus, and fecal pellets. Shapes ranged from comets (Fig. 1d) to spheroids (Fig. 1c) to oblate spheres (Fig. 1b). Some of the aggregates had irregular shapes or contained abundant macrocrustacean (primarily euphausiid) fecal pellets (Fig. 1e). The shapes of some aggregates appeared to have been deformed by the flow of fluid around them as they sank (Fig. 1b, d). Sinking aggregates maintained a stable orientation in the water, and we observed no twisting or rotating as they sank.

Diameters of the aggregates ranged from 0.5 to 25.5 mm and maximum lengths from 2.4 to 75 mm. Aggregate volumes ranged from 3 to 6,000 mm^3 and were related to approximately the cube of aggregate diameter (Fig. 2A). Dry weights varied from 2 to 1,110 μg aggregate^{-1} and also increased significantly with aggregate diameter (Fig. 2B). Projected areas ranged from 0.1 to 511 mm^2. Reynolds numbers ranged from 0.4 to 32.

The aggregates studied had very high porosities ranging from 97 to 99.9% with a mean of 99.5%. Porosity increased significantly with increasing particle diameter (Fig. 2C). We plotted the log of (1 − porosity), as did Kajihara (1971), in order to reveal the large range of porosities encountered (Fig. 2C).

The excess density ($\Delta\rho$) of the aggregates ranged over four orders of magnitude from 2.2×10^{-2} to 1.3×10^{-5} g cm^{-3} (Fig. 2D). The median was 1.4×10^{-4} g cm^{-3}. Only 20% of the aggregates had a $\Delta\rho > 1 \times 10^{-3}$ g cm^{-3} (Fig. 2D). If we assume that the interstitial water within the aggregates had the same density as the surrounding seawater, or 1.02488 g cm^{-3}, the median absolute density of the aggregates of marine snow collected at our study sites was 1.02502 g cm^{-3}. Excess density was highly correlated with aggregate size (Fig. 2D) despite the variable nature of the primary particles comprising the aggregates—including varying proportions of fecal pellets, mucus, molts, frustules, and other components. Although it appeared that diatom flocs might have a different excess density to size relationship than other types of marine snow, the slope of the regression line describing that relationship was not significantly different (ANCOVA test for equality of slope: Sokal and Rohlf 1969) from the slope of the regression line describing the excess density to size relationship for all of the other aggregates (Fig. 2D). The data set for diatom snow was small with high variability, however, so additional data may reveal a significant difference.

Settling velocities—Figure 3 displays the settling velocities of 80 aggregates of marine

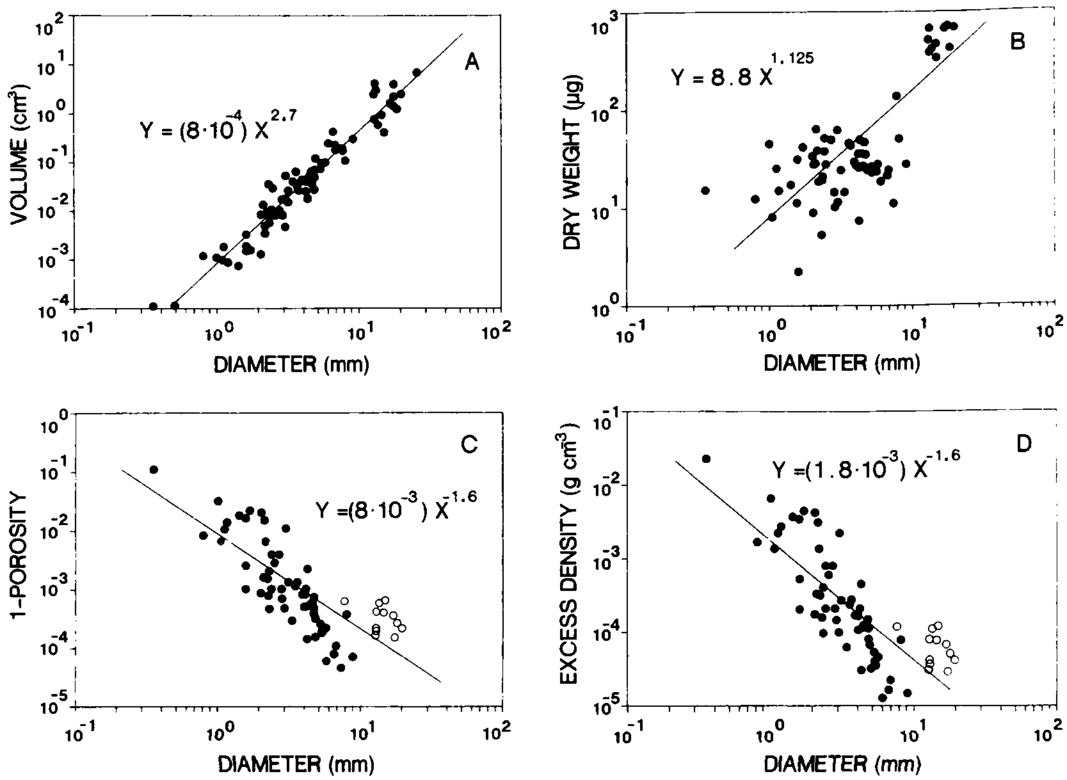


Fig. 2. Size characteristics of marine snow. A. Aggregate volume as a function of diameter (regression coefficient, rc, = 0.97; $P < 0.001$). B. Aggregate dry weight as a function of diameter (rc = 0.71; $P < 0.001$). C. Aggregate porosity as a function of diameter: O—diatom flocs; ●—all other marine snow regardless of origin (rc = 0.79; $P < 0.001$). D. Aggregate excess density as a function of diameter (rc = 0.79; $P < 0.001$), symbols as in panel C.

snow in situ as a function of various particle characteristics. Mean settling rate was 74 ± 39 m d^{-1}. Sinking speed increased exponentially with particle diameter (Fig. 3A). Settling velocities increased with the increasing ratio of volume to projected area, as predicted by settling theory (Fig. 3B).

Settling rate in situ increased exponentially with aggregate dry weight (Fig. 3C). We compared the size-specific settling rates of marine snow determined in the laboratory with rates for similarly sized and shaped aggregates determined in situ with dry weight as an accurate measure of aggregate size. Despite minimal handling of particles, settling velocities measured in the laboratory were consistently higher, by up to four times, than those of similarly sized aggregates measured in situ (Fig. 3C). No significant statistical correlation could be found between sinking rate and dry weight of aggregates studied in the laboratory.

Although settling theory predicts that the sinking rate of an object settling in a fluid is a function of the excess density of the object, our data did not yield a significant relationship between excess aggregate density, as calculated by our methods, and sinking rate (Fig. 3D).

We measured or derived all of the dimensional terms in the force balance Eq. 1 for a settling object. Thus, we can directly calculate the drag coefficient, C_D, for each sinking aggregate. Calculations of C_D for our nonspherical aggregates can provide insight into the effects of shape and other variables that potentially alter the settling behavior of marine snow relative to sinking spheres.

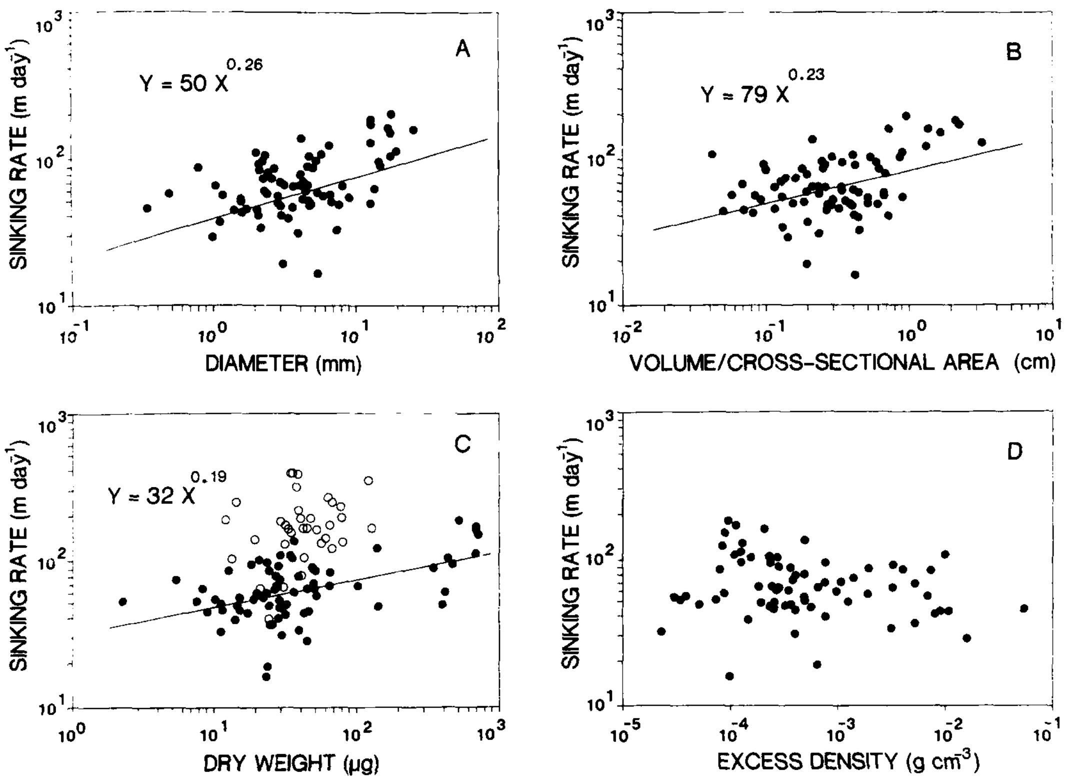


Fig. 3. Sinking rates of marine snow in situ (●) as a function of: A—aggregate diameter (regression coefficient, rc, = 0.61; $P < 0.001$); B—aggregate volume divided by projected area (rc = 0.42; $P < 0.001$); C—aggregate dry weight (rc = 0.60; $P < 0.001$) (O—sinking velocities determined in the laboratory); D—aggregate excess density.

Figure 4A presents C_D as a function of Reynolds number. Also plotted on Fig. 4A are the predicted curves for spheres assuming Stokes settling ($C_D = 24/\mathrm{Re}$) and an empirically determined relationship,

$$C_D = \frac{24}{\mathrm{Re}} + \frac{6}{1 + (\mathrm{Re})^{1/2}} + 0.4, \qquad (7)$$

for solid spheres at higher Reynolds numbers (White 1974).

The drag coefficients of marine snow were consistently higher than those of spheres of equivalent Reynolds number (Fig. 4A), indicating that marine snow sank more slowly than equivalent spheres. Spheres sink more rapidly than most other shapes (Simpson 1982). Moreover, for nonspherical particles, C_D is a function of both Re and shape. Therefore, we investigated shape as a factor affecting settling velocity.

We hypothesized that the coefficient of form resistance, k, would also increase with increasing nonsphericity for marine snow particles. We determined the Corey shape factor, CSF, assuming that the particles were symmetrical about their polar axis; thus the two smallest axial diameters, D_s and D_i, were equal for prolate aggregates while D_i and D_l were equal for oblate aggregates. We calculated U_s, the settling velocity of a sphere of equivalent volume and density to each aggregate, with the force balance Eq. 2. In solving this equation for equivalent spheres, we used the equation for C_D empirically derived by White (Eq. 7) for spheres outside the Stokes range. Since excess density was size-specific, we used the empirically derived function of Fig. 2D to calculate the excess density of sinking spheres as a function of sphere diameter. Substitution of these parameters into the force balance Eq. 2 enabled us to obtain a solution for the settling velocity of a sphere with a volume and density equivalent to each aggregate of marine snow.

We found no significant relationship between k and the shapes of the aggregates (Fig. 4B). We also found no relationship when the analysis was restricted to oblate aggregates or prolate aggregates only. Aggregates whose shapes varied greatly from spherical, including long comets, had values of k very similar to those of nearly spherical particles. Some near-spherical aggregates sank considerably slower than equivalent spheres, with values of $k \gtrsim 3$, rather than the predicted value of 1. Previous studies on the effects of shape on C_D predict that particles with highly nonsperhical shapes would have higher drag coefficients (Komar and Reimers 1978), but we found no significant relationship between shape and C_D (Fig. 4C).

The C_D of marine snow was higher than predicted for sinking spheres of equivalent Reynolds number, since the settling velocity of marine snow was slower than that of equivalent spherical particles. Although we found no relationship between either drag coefficient or the coefficient of form resistance and the Corey shape factor, shape might still partially explain the high C_D observed. Other factors including permeability and surface roughness might also increase drag.

In order to elucidate these issues, we plotted the sinking velocity of particles of several different shapes and porosities having volumes and excess densities equivalent to those of our aggregates (Fig. 5). The equations for the settling velocities of a sphere, and a prolate ellipsoid with an aspect ratio of 4 : 1 [prolate ellipsoid (a) based on Stokes' law, Fig. 5] were obtained from Lerman et al. (1974). The settling velocities of equivalent spheres at Reynolds numbers outside the Stokes range (Re > 0.5) were obtained from White (1974) as described previously. The empirically derived curve for the settling velocity of equivalent prolate ellipsoids with aspect ratio of 4 : 1 at Re > 0.5 [prolate ellipsoid (b), Fig. 5] was obtained by solving Eq. 4 for the settling velocity, U, of a prolate ellipsoid by using the settling

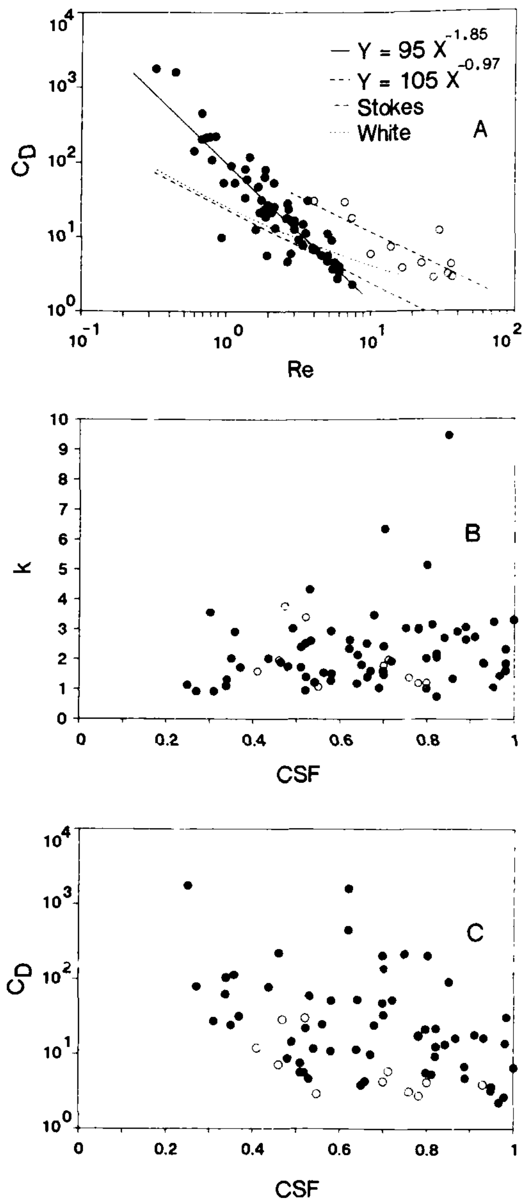


Fig. 4. Drag coefficient (C_D) and effects of shape (○—diatom snow; ●—marine snow of all other origins). A. C_D vs. Reynolds number (Re); White—C_D of sinking spheres determined empirically from White (1974); Stokes—C_D, as predicted by Stokes' equation. B. The dynamic shape factor, k, as a function of the Corey shape factor (CSF). CSF should equal 1 for perfect spheres (*see text for definitions*). C. Drag coefficient as a function of the Corey shape factor.

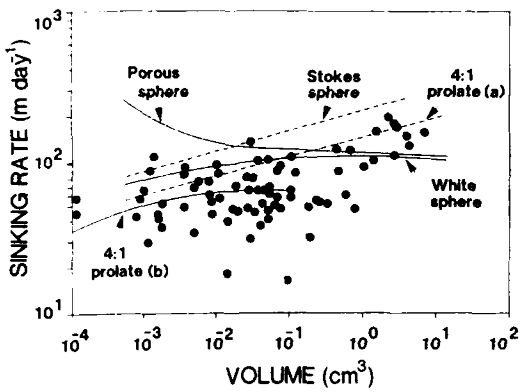


Fig. 5. Settling velocities of marine snow (●) and of various spheres and prolate ellipsoids with volumes and excess densities equal to those of the aggregates studied. Dashed lines are theoretical settling rates predicted by Stokes' ("Stokes sphere") or variations of Stokes' law for prolate ellipsoids, prolate 4:1 (a). Solid lines are settling velocities derived from empirical studies. "White sphere," solid spheres according to White (1974). Porous spheres predicted from empirical data of Matsumoto and Suganuma (1977). Prolate 4:1 (b) predicted from empirical data of White (1974) with k values from McNown and Malaika (1950) to correct for nonspherical shape.

velocities of sinking spheres (U_s) from White (1974) and k values for a prolate ellipsoid of 4 : 1 aspect ratio from McNown and Malaika (1950) who empirically determined k up to Re of ~10.

In order to estimate the potential effects of permeability on settling velocities of marine snow, we used data on permeable flocs of steel wool ranging in porosity from 90 to 99.7% and in size from 3 to 100 mm studied by Matsumoto and Suganuma (1977). The settling velocities of permeable steel wool flocs having volumes and densities equivalent to those of the marine snow were calculated by correcting sinking rates of solid equivalent spheres as determined with White's equation, using the size-specific correction factor, F, developed empirically by Matsumoto and Suganuma (1977).

Figure 5 demonstrates that aggregates sink considerably more slowly than do spheres and 4 : 1 prolate spheres of equivalent volume and excess density as predicted with Stokes' law. Aggregates sink, on average, only about half as fast, however, as would be expected for equivalent spheres at Reynolds numbers >1. Porosity appears to increase, rather than decrease, sinking velocities within the range studied. The porous spheres of Matsumoto and Suganuma (1977) had rough, convoluted surfaces analogous to the surfaces of marine snow aggregates. Such convoluted surfaces might increase skin friction and thus total drag on the particle. Neither surface roughness nor permeability, however, appears to have increased the drag of Matsumoto and Suganuma's particles. Masliyah and Polikar (1980) also investigated the settling velocities of permeable spheres of milled plastic up to 2.5 cm in diameter and at Re up to 120. These spheres were 97% porous with highly convoluted and prickly surfaces. Their settling velocities also deviated only slightly from the settling velocities of equivalent impermeable spheres. Thus permeability and surface roughness probably have relatively little effect on the settling velocities of marine snow. Logan and Hunt (1987) concluded that surface roughness and flow through microbial aggregates probably did not contribute to observed deviations in settling velocity compared to predictions for impermeable spheres.

Discussion

Many different methods have been used to estimate the sinking rates of marine snow. Our sinking rates tended to be lower than those estimated from time-lapse photography of the seafloor (100–150 m d^{-1}: Billett et al. 1983; Lampitt 1985) and lower than those measured by ourselves and others in settling chambers in the laboratory (Silver and Alldredge 1981; Taguchi 1982; Gorsky et al. 1983). Collection and gentle transfer of fragile aggregates in the laboratory apparently result in slight collapse of the aggregate, with concurrent decreases in porosity, increases in density, and increases in settling velocity. Our sinking rates were similar to the range of 43–95 m d^{-1} reported by Shanks and Trent (1980), who measured sinking rates of aggregates in large cylinders in situ. In general, we observed similar sinking rates to those calculated by Asper (1986) from sediment trap data and particle abundances in the water column, although we never observed rates as low as the 1 m d^{-1} he reported from deep water of the Panama Basin. The highly porous, flocculent nature of the material he observed may explain its slow sinking rate.

Previous investigations of the settling velocities of natural aggregated matter as a function of aggregate diameter vary somewhat from our results. Kajihara (1971) found $U = 160d^{0.57}$ and Gibbs (1985) reported $U = 248d^{0.78}$ respectively for reaggregated and estuarine flocs of <1 mm; we report $U = 50d^{0.26}$ for marine snow aggregates of larger size.

Previous investigations of the porosity and excess density of natural and manmade flocs have yielded results similar to those reported here. Assuming Stokes' law, Kajihara (1971) claculated the porosity of natural marine flocs <1 mm from settling velocities measured in the laboratory. He found that porosity increased with increasing particle size, although he reported porosities lower than ours for similarly sized particles. His particles were formed by reaggregation of smaller component particles and were probably more dense than natural flocs. Gibbs (1985) found that excess density of estuarine flocs <1 mm decreased with increasing floc size. Tambo and Watanabe (1979) also found decreasing excess density with increasing size for clay-aluminum flocs in the laboratory, although the excess density of these inorganic flocs was about three times that of marine snow aggregates of equivalent size. Our empirical result that porosity of marine snow increases in proportion to $d^{-1.6}$ corroborates the independently derived assumption of Logan and Hunt (1987) that the porosity of microbial flocs increases in proportion to $d^{-1.6}$.

We observed a large range and high scatter of settling velocities when plotted against diameter and dry weight—parameters that could be measured with minimal error. This scatter most likely arose from error in measuring sinking rates in situ (variations in exact sinking distance, etc.) and from the highly heterogeneous nature of the aggregates themselves. Aggregate size, shape, composition (i.e. presence of fecal pellets, mucus, diatoms, etc.), porosity, and rigidity were all highly variable in the population of natural and randomly chosen particles studied here, resulting in a large range of sinking rates. Plots of settling velocity vs. size for natural microscopic particles of sediment of uniform composition show scatter similar to that which we observed for macroscopic aggregates (Hawley 1982).

Nonspherical shapes result in decreased settling velocities of aggregates in all the cases examined in Fig. 5. In fact, when nonspherical shape is taken into account, macroscopic aggregates appear to sink within the range predicted for similar nonspherical particles sinking outside the Stokes range [Fig. 5, curve 4:1 prolate (b)]. Thus, deviations in the settling rate of marine snow from that of spheres at Reynolds numbers >1 may result partly from deviations from nonspherical shape. Why then did we not obtain significant relationships between settling velocity and either shape or excess density?

The coefficient of form resistence (k) and settling velocity both depend on excess density. Excess density is directly dependent on the primary particle density (*see Eq. 6*). We assumed that this primary particle density was a constant for all aggregates and equal to the wet density of euphausiid fecal pellets—the only density value we could find in the literature for a natural marine particle with components similar to those of marine snow. This assumption probably resulted in sufficient error to obscure the expected relationship between sinking and shape and excess density of marine snow.

Assumption of a constant primary particle density for all marine snow aggregates is problematic for two major reasons. First, the primary particles composing marine snow aggregates are not homogeneous. Diatom frustules, clay mineral particles, fecal pellets, living phytoplankton, protozoa, crustacean carapaces, and the various unidentifiable debris making up marine snow each have their own densities. Each aggregate is composed of varying percentages of these and other components yielding its own, unique total excess density. To accurately determine the excess density of each aggregate we would have to know not only the exact composition and size of each component particle comprising it, but also the densities of those components. Reliable data of this sort are not currently available for any of the complex types of natural particles composing marine snow.

Second, the problem of determining the

density of the component particles in marine snow is further confounded by the sizable percentage of living organisms comprising some aggregates (Silver et al. 1978). Many of these organisms can regulate their individual buoyancies. Diatom flocs represent an extreme type of marine snow where >90% of the particle may be living cells (Alldredge unpubl.). The density of diatoms varies with their physiological state and even with the time of day (Eppley et al. 1967; Smayda 1970). When nutrient replete, diatom cells may be neutrally buoyant. When nutrient stressed their excess density ranges up to 0.08 g cm^{-3} (Eppley et al. 1967). It is probable that we overestimated the excess density of the diatom flocs because we assumed they had a constant primary particle density similar to other aggregates that contain a much lower proportion of living cells. This assumption may have produced the apparent deviations in porosity, excess density, and drag coefficient observed for this type relative to other types of marine snow. Aggregates are not composed solely of inanimate particles, and thus, we would expect their overall density to depend, in part, on the density of their living components. This density may vary on a scale as short as hours, depending upon the nature of the community on the snow and its physiological state. Clearly additional research on the density of natural marine particles is needed to refine the relationships between sinking and aggregate characteristics reported here.

Relationships between sinking and both excess density and shape may also have been obscured by high scatter in the data and by the compounding of error in the measurements. Excess density is dependent on volume and dry weight—each with its own corresponding errors. The odd finding that some of the values for the drag coefficients of marine snow are lower than those predicted by Stokes' law may also arise from compounding of random error since the calculation of drag coefficient depends on several empirically determined variables including settling velocity, projected area, and excess density.

Data provided herein may allow estimation of the characteristics and flux of natural particles based on their size distributions in situ generated from photographs and survey cameras (*see* Asper 1987; Johnson and Wangersky 1985). Estimates of particulate flux based on collection of particles in the water column with in situ pumps have already provided considerable information about flux (Bishop et al. 1977, 1980). Care must be taken in calculating flux from predicted settling rates and measured particle abundances in the water column, however. Just because large particles sink does not necessarily mean that they sink out of the water column at the predicted rate. Accumulation of marine snow has been documented at a well-developed pycnocline in the subtropical Atlantic (Alldredge and Youngbluth 1985). Marine snow accumulating at the top of a density discontinuity could be reinjected back into the mixed layer by wind-mixing events. Reinjection of some proportion of the marine snow population back into the mixed layer would result in accumulation of marine snow in surface waters and potential residence times for these particles longer than would be predicted based on their sinking rates alone. Macrocrustacean fecal pellets, particles with settling velocities and excess densities considerably greater than those of marine snow, are known to have residence times in surface waters up to 10 d or more (Alldredge et al. 1987). Moreover, lateral advection appears responsible for high snow abundances at certain depths in the Panama Basin (Asper 1986); aggregates are carried horizontally as well as sinking vertically. Since flux calculations often assume that the particles immediately sink out of the system, calculations of particulate flux based on particle abundances and size distributions in situ and on predicted settling velocities could overestimate flux to the ocean interior and to the seafloor.

References

ALBERTSON, M. 1953. Effects of shape on the fall velocity of gravel particles, p. 243–261. Proc. 5th Iowa Hydraul. Conf.

ALLDREDGE, A. L., C. C. GOTSCHALK, AND S. MACINTYRE. 1987. Evidence for sustained residence of macrocrustacean fecal pellets in surface waters off southern California. Deep-Sea Res. **34**: 1641–1652.

———, AND M. J. YOUNGBLUTH. 1985. The significance of macroscopic aggregates (marine snow) as sites for heterotrophic bacterial production in the mesopelagic zone of the subtropical Atlantic. Deep-Sea Res. **32:** 1445–1456.

ANGEL, M. V. 1984. Detrital organic fluxes through pelagic ecosystems, p. 425–516. *In* Flows of energy and materials in marine ecosystems, theory and practice. NATO Conf. Ser. 4, Mar. Sci. V. 13. Plenum.

ASPER, V. L. 1986. Accelerated settling of marine particulate matter by "marine snow" aggregates. Ph.D. thesis, Mass. Inst. Technol./Woods Hole Oceanogr. Inst. WHOI-96-12. 189 p.

———. 1987. Measuring the flux and sinking speed of marine snow aggregate . Deep-Sea Res. **34:** 1–18.

BILLETT, D. S. M., R. S. LAMPITT, A. L. RICE, AND R. F. C. MANTOURA. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature **302:** 520–522.

BISHOP, J. K. B., R. W. COLLIER D. R. KETTEN, AND J. M. EDMOND. 1980. The chemistry, biology and vertical flux of particulate matter from the upper 400 m of the Panama Basin. Deep-Sea Res. **27:** 615–640.

———, J. M. EDMOND, D. R. KETTEN, M. P. BACON, AND W. B. SILKER. 1977. The chemistry, biology and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. Deep-Sea Res. **24:** 511–548.

DAVIS, C. N. 1979. Particle-fluid interaction. J. Aerosol Sci. **10:** 477–513.

EPPLEY, R. W., R. W. HOLMES, AND J. D. H. STRICKLAND. 1967. Sinking rates of marine phytoplankton measured with a fluorometer. J. Exp. Mar. Biol. Ecol. **1:** 191–208.

FOK-PUN, L., AND P. D. KOMAR. 1983. Settling velocities of planktonic foraminifera: Density variations and shape effects. J. Foram. Res. **13:** 60–68.

FOWLER, S. W., AND G. A. KNAUER. 1986. Role of large particles in transport of elements and organic compounds through the oceanic water column. Prog. Oceanogr. **16:** 147–194.

GIBBS, R. J. 1985. Estuarine flocs: Their size, settling velocity and density. J. Geophys. Res. **90:** 3249–3251.

GORSKY, G., N. S. FISHER, AND S. W. FOWLER. 1983. Biogenic debris from the pelagic tunicate, *Oikopleura dioica*, and its role in the vertical transport of a transuranium element. Estuarine Coastal Shelf Sci. **18:** 13–23.

GRAF, W. H. 1971. Hydraulics of sediment transport. McGraw-Hill.

HAWLEY, N. 1982. Settling velocity distribution of natural aggregates. J. Geophys. Res. **87:** 9489–9498.

HUTCHINSON, G. E. 1967. A treatise on limnology. V. 2. Wiley.

JOHNSON, B. D., AND P. J. WANGERSKY. 1985. A recording backward scattering meter and camera system for examination of the distribution and morphology of macroaggregates. Deep-Sea Res. **32:** 1143–1150.

KAJIHARA, M. 1971. Settling velocity and porosity of large suspended particles. J. Oceanogr. Soc. Jpn. **27:** 158–162.

KOMAR, P. D., A. P. MORSE, AND L. F. SMALL. 1981. An analysis of sinking rates of natural copepod and euphausiid fecal pellets. Limnol. Oceanogr. **26:** 172–180.

———, AND C. E. REIMERS. 1978. Grain shape effects on settling rates. J. Geol. **86:** 193–209.

LAMPITT, R. S. 1985. Evidence for the seasonal deposition of detritus for the deep-sea floor and its subsequent resuspension. Deep-Sea Res. **32:** 885–897.

LERMAN, A., L. DEVENDRA, AND M. F. DACEY. 1974. Stokes' settling and chemical reactivity of suspended particles in natural waters, p. 17–47. *In* R. J. Gibbs [ed.], Suspended solids in water. Plenum.

LOGAN, B. E., AND J. R. HUNT. 1987. Advantages to microbes of growth in permeable aggregates in marine systems. Limnol. Oceanogr. **32:** 1034–1048.

MCNOWN, J. S., AND J. MALAIKA. 1950. Effects of particle shape on settling velocity at low Reynolds numbers. Trans. Am. Geophys. Union **31:** 74–82.

MAMAYEV, O. I. 1975. Temperature-salinity analysis of world ocean waters. Elsevier.

MASLIYAH, J. H., AND M. POLIKAR. 1980. Terminal velocity of porous spheres. Can. J. Chem. Eng. **58:** 299–302.

MATSUMOTO, K., AND A. SUGANUMA. 1977. Settling velocity of a permeable model floc. Chem. Eng. Sci. **32:** 445–447.

SHANKS, A. L., AND J. D. TRENT. 1980. Marine snow: Sinking rates and potential role in vertical flux. Deep-Sea Res. **27:** 137–144.

SILVER, M. W., AND A. L. ALLDREDGE. 1981. Bathypelagic marine snow: Deep-sea algal and detrital community. J. Mar. Res. **39:** 501–530.

———, A. L. SHANKS, AND J. D. TRENT. 1978. Marine snow: Microplankton habitat and source of small-scale patchiness in pelagic populations. Science **201:** 371–373.

SIMPSON, W. R. 1982. Particulate matter in the oceans—sampling methods, concentration, size distribution and particle dynamics. Oceanogr. Mar. Biol. Annu. Rev. **20:** 119–172.

SMAYDA, T. R. 1970. The suspension and sinking of phytoplankton in the sea. Oceanogr. Mar. Biol. Annu. Rev. **8:** 355 p. Allen & Unwin.

SMETACEK, V. S. 1985. Role of sinking in diatom life-history cycles: Ecological, evolutionary and geological significance. Mar. Biol. **84:** 239–251.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. Freeman.

TAGUCHI, S. 1982. Seasonal study of fecal pellets and discarded houses of appendicularia in a subtropical inlet, Kaneohe Bay, Hawaii. Estuarine Coastal Shelf Sci. **14:** 545–555.

TAMBO, N., AND Y. WATANABE. 1979. Physical characteristics of flocs—1. The floc density function and aluminum floc. Water Res. **13:** 409–419.

TIETJENS, O. G. 1957. Applied hydro- and aeromechanics. Dover.

WHITE, F. M. 1974. Viscous fluid flow. McGraw-Hill.

Submitted: 13 February 1987
Accepted: 7 December 1987
Revised: 23 February 1988

mesopelagic zone of the subtropical Atlantic. Deep-Sea Res. **32:** 1445–1456.

ANGEL, M. V. 1984. Detrital organic fluxes through pelagic ecosystems, p. 425–516. *In* Flows of energy and materials in marine ecosystems, theory and practice. NATO Conf. Ser. 4, Mar. Sci. V. 13. Plenum.

ASPER, V. L. 1986. Accelerated settling of marine particulate matter by "marine snow' aggregates. Ph.D. thesis, Mass. Inst. Technol./Woods Hole Oceanogr. Inst. WHOI-96-12. 189 p.

———. 1987. Measuring the flux and sinking speed of marine snow aggregates. Deep-Sea Res. **34:** 1–18.

BILLETT, D. S. M., R. S. LAMPITT, A. L. RICE, AND R. F. C. MANTOURA. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature **302:** 520–522.

BISHOP, J. K. B., R. W. COLLIER D. R. KETTEN, AND J. M. EDMOND. 1980. The chemistry, biology and vertical flux of particulate matter from the upper 400 m of the Panama Basin. Deep-Sea Res. **27:** 615–640.

———, J. M. EDMOND, D. R. KETTEN, M. P. BACON, AND W. B. SILKER. 1977. The chemistry, biology and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. Deep-Sea Res. **24:** 511–548.

DAVIS, C. N. 1979. Particle-fluid interaction. J. Aerosol Sci. **10:** 477–513.

EPPLEY, R. W., R. W. HOLMES, AND J. D. H. STRICKLAND. 1967. Sinking rates of marine phytoplankton measured with a fluorometer. J. Exp. Mar. Biol. Ecol. **1:** 191–208.

FOK-PUN, L., AND P. D. KOMAR. 1983. Settling velocities of planktonic foraminifera: Density variations and shape effects. J. Foram. Res. **13:** 60–68.

FOWLER, S. W., AND G. A. KNAUER. 1986. Role of large particles in transport of elements and organic compounds through the oceanic water column. Prog. Oceanogr. **16:** 147–194.

GIBBS, R. J. 1985. Estuarine flocs: Their size, settling velocity and density. J. Geophys. Res. **90:** 3249–3251.

GORSKY, G., N. S. FISHER, AND S. W. FOWLER. 1983. Biogenic debris from the pelagic tunicate, *Oikopleura dioica,* and its role in the vertical transport of a transuranium element. Estuarine Coastal Shelf Sci. **18:** 13–23.

GRAF, W. H. 1971. Hydraulics of sediment transport. McGraw-Hill.

HAWLEY, N. 1982. Settling velocity distribution of natural aggregates. J. Geophys. Res. **87:** 9489–9498.

HUTCHINSON, G. E. 1967. A treatise on limnology. V. 2. Wiley.

JOHNSON, B. D., AND P. J. WANGERSKY. 1985. A recording backward scattering meter and camera system for examination of the distribution and morphology of macroaggregates. Deep-Sea Res. **32:** 1143–1150.

KAJIHARA, M. 1971. Settling velocity and porosity of large suspended particles. J. Oceanogr. Soc. Jpn. **27:** 158–162.

KOMAR, P. D., A. P. MORSE, AND L. F. SMALL. 1981. An analysis of sinking rates of natural copepod and euphausiid fecal pellets. Limnol. Oceanogr. **26:** 172–180.

———, AND C. E. REIMERS. 1978. Grain shape effects on settling rates. J. Geol. **86:** 193–209.

LAMPITT, R. S. 1985. Evidence for the seasonal deposition of detritus for the deep-sea floor and its subsequent resuspension. Deep-Sea Res. **32:** 885–897.

LERMAN, A., L. DEVENDRA, AND M. F. DACEY. 1974. Stokes' settling and chemical reactivity of suspended particles in natural waters. p. 17–47. *In* R. J. Gibbs [ed.]. Suspended solids in water. Plenum.

LOGAN, B. E., AND J. R. HUNT. 1987. Advantages to microbes of growth in permeable aggregates in marine systems. Limnol. Oceanogr. **32:** 1034–1048.

MCNOWN, J. S., AND J. MALAIKA. 1950. Effects of particle shape on settling velocity at low Reynolds numbers. Trans. Am. Geophys. Union **31:** 74–82.

MAMAYEV, O. I. 1975. Temperature-salinity analysis of world ocean waters. Elsevier.

MASLIYAH, J. H., AND M. POLIKAR. 1980. Terminal velocity of porous spheres. Can. J. Chem. Eng. **58:** 299–302.

MATSUMOTO, K., AND A. SUGANUMA. 1977. Settling velocity of a permeable model floc. Chem. Eng. Sci. **32:** 445–447.

SHANKS, A. L., AND J. D. TRENT. 1980. Marine snow: Sinking rates and potential role in vertical flux. Deep-Sea Res. **27:** 137–144.

SILVER, M. W., AND A. L. ALLDREDGE. 1981. Bathypelagic marine snow: Deep-sea algal and detrital community. J. Mar. Res. **39:** 501–530.

———, A. L. SHANKS, AND J. D. TRENT. 1978. Marine snow: Microplankton habitat and source of small-scale patchiness in pelagic populations. Science **201:** 371–373.

SIMPSON, W. R. 1982. Particulate matter in the oceans—sampling methods, concentration, size distribution and particle dynamics. Oceanogr. Mar. Biol. Annu. Rev. **20:** 119–172.

SMAYDA, T. R. 1970. The suspension and sinking of phytoplankton in the sea. Oceanogr. Mar. Biol. Annu. Rev. **8:** 355 p. Allen & Unwin.

SMETACEK, V. S. 1985. Role of sinking in diatom life-history cycles: Ecological, evolutionary and geological significance. Mar. Biol. **84:** 239–251.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. Freeman.

TAGUCHI, S. 1982. Seasonal study of fecal pellets and discarded houses of appendicularia in a subtropical inlet, Kaneohe Bay, Hawaii. Estuarine Coastal Shelf Sci. **14:** 545–555.

TAMBO, N., AND Y. WATANABE. 1979. Physical characteristics of flocs—1. The floc density function and aluminum floc. Water Res. **13:** 409–419.

TIETJENS, O. G. 1957. Applied hydro- and aeromechanics. Dover.

WHITE, F. M. 1974. Viscous fluid flow. McGraw-Hill.

Submitted: 13 February 1987
Accepted: 7 December 1987
Revised: 23 February 1988